# THE EFFECTS OF ARTIFICIAL REEF VERTICAL PROFILE AND HOLE DIAMETER ON FISHES OFF SOUTH CAROLINA

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#### ABSTRACT

Attraction of demersal finfish to six artificial reef designs off Charleston, South Carolina, was studied using a SCUBA visual census technique. The experiment was designed to examine the effect of (1) increased vertical profile and (2) hole diameter on the recruitment and retention of demersal finfish to each of the six artificial reef designs. Increased vertical profile was accomplished through the addition of fish aggregation devices (FADs) to half of the benthic artificial reef units, which were concurrently equipped with large diameter holes (25.4 cm diameter), small diameter holes (12.7 cm diameter), or no holes. Mean abundances of demersal finfish individuals were significantly greater on FAD units than on units lacking FADs. Hole diameter was only occasionally a significant factor affecting mean total number of demersal individuals and species and did not significantly affect estimated average total lengths of species present. Hole presence (both hole diameters) had a positive significant affect on mean numbers of demersal individuals and species. The dominant species observed on the reefs included Decapterus punctatus, Stenotomus chrysops, Centropristis striata, Monacanthus hispidus, and Haemulon aurolineatum. Early observations of the unit designs have already prompted the South Carolina Marine Artificial Reef Program to deploy artificial reef units of the same design in a permitted reef site.

Natural reefs are aquatic habitats that offer topographic relief and are usually characterized by high taxonomic diversity relative to their surroundings (Fagerstrom, 1987). Reefs typically support large numbers of algal, invertebrate, and fish species (Bohnsack and Sutherland, 1985; Buckley and Hueckel, 1985; Mottet, 1985).

Artificial reefs are used in marine and freshwater environments in an attempt to mimic the floral and faunal productivity of natural reefs. An artificial reef is a purposefully or accidentally deployed man-made structure that offers topographic relief in an aquatic habitat. Artificial reefs, like natural reefs, are characterized by high taxonomic diversity relative to their surroundings (Bohnsack et al., 1994). Artificial reefs are used not only to enhance fishing success (Turner et al., 1969; Dewees and Gotshall, 1974), but also are being explored for use as mitigation for habitat alteration or loss (Stone, 1982; Davis, 1985; Spanier et al., 1985; Hueckel et al., 1989; Seaman et al., 1989).

Historically, the placement of artificial reefs in U.S. waters has been based primarily on (1) the availability and cost of disposable scrap materials and (2) the occurrence of accidental shipwrecks (Valentry, 1968; Bohnsack and Sutherland, 1985; Seaman et al., 1989). However, scrap materials are normally not designed to persist in aquatic environments. "Scrap" reefs may therefore be detrimental to reef site flora and fauna if reef materials degrade and pollutants are released into the water column (Duedall et al., 1985). As the availability and cost-effectiveness of suitable scrap materials for artificial reefs declines, more attention is being focused on prefabricated reefs. Prefabricated reefs can be designed specifically to attract particular species and sizes of fishes by altering design parameters such as reef size, complexity, and amount of vertical relief (Sheehy, 1982;

Bell et al., 1989). Continued research is essential to the design and development of artificial reefs that are useful in fishery management programs.

The main purpose of this study was to examine the effects of increased vertical profile on demersal finfish recruitment and retention to benthic artificial reefs. The increase in vertical profile was accomplished by the addition of Fish Aggregation Devices (FADs) to experimental benthic reef units. FADs are structures that create floating artificial habitats which are suspended at the surface, slightly below the surface, or in midwater between the surface and the bottom. Past studies have shown that the amount of vertical profile present on artificial and natural reefs can affect the number of demersal and pelagic fish species and individuals present on that reef (Ogawa, 1967; Molles, 1978; Myatt, 1981; Beets, 1989; Matthews, 1990). Beets (1989) reported that benthic artificial reefs associated with midwater FADs attracted significantly more benthic species and nominally more benthic individuals than benthic artificial reefs without FADs. While the effects of vertical profile have been the topic of many artificial reef studies, scant information exists regarding the effect of FADs on benthic reef-associated fishes. Two studies performed off the South Carolina coast have suggested that the presence of midwater FADs increased numbers of finfish individuals and species around benthic units (Hammond et al., 1977; Rountree, 1989). Rountree (1987, 1990) found that the fauna associated with the remaining anchors of destroyed FADs was significantly more depauperate than the fauna associated with anchors with attached FADs. The results of Rountree (1987, 1990) suggested that pelagic fish assemblages associated with FADs affect the abundance and diversity of demersal fishes associated with FAD anchors. In the same manner, FADs may affect the demersal fish assemblages associated with benthic artificial reefs.

A second purpose of the study was to examine the effects of increased complexity on finfish recruitment and retention through the addition of holes with various diameters to the experimental benthic units. Many authors have studied the relationships between shelter and reef-associated fishes (Randall, 1963; Robertson and Sheldon, 1979; Buckley, 1982; Shulman, 1984, Zahary and Hartman, 1985; Hixon and Beets, 1989). The complexity of an artificial reef can affect finfish community establishment on that reef. Complexity of reef structures can be increased by the addition of cavities or holes, which may provide shelter from predation and can increase juvenile recruitment, numbers of species, and total fish density on artificial reefs (Shulman, 1984). Thus, we investigated the effects of hole diameter and hole presence on the recruitment and retention of fishes to benthic artificial reefs.

A third purpose of this study was to quantify the sequential recruitment of finfish species to the experimental reef designs. Data regarding the temporal sequence of fish fauna attracted to artificial reefs can become a valuable tool for devising management plans that utilize artificial reef technology.

#### MATERIALS AND METHODS

The study was conducted near the Capers Artificial Reef approximately 23 km northeast of Charleston, South Carolina (32°45.20'N, 79°34.15'W). The site is characterized by flat sandy bottom that is devoid of relief, large sessile invertebrates (sponges, cnidarians, etc.), and obvious algal growth. The study site was left unmarked to reduce the likelihood that fishing would take place in the general area.

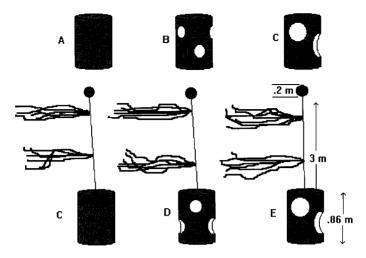


Figure 1. Six artificial reef designs, showing: (A) HN unit, (B) HP unit with small holes, (C) HP unit with large holes, (D) HN unit with FAD, (E) HP unit with small holes and FAD, and (F) HP unit with large holes and FAD.

The vertical profile of 15 prefabricated benthic units was increased by the addition of a single FAD to each of those units. Each FAD consisted of approximately 250 cm of 91 kg (200 lb) test monofilament line, a 0.2 m diameter crab pot float, and two sets of plastic streamers (Fig. 2). FADs reached a height of approximately 3 m into the water column above the benthic units. Each benthic unit consisted of one 208.2 L (55 gal) drum weighted with approximately 227 kg of concrete. Benthic units had a vertical profile of 0.86 m and a diameter of 0.58 m. Benthic units of three designs were used: units with "large" diameter holes (diameter = 25.4 cm), units with "small" diameter holes (diameter = 12.7 cm), and units with no holes. The units with no holes were included to serve as a control group. Analyses were performed to determine whether hole diameter (large vs small vs no holes) and hole presence (holes present vs holes absent) had a significant effect on finfish individual abundance, species richness, and estimated average total length.

In the Results and Discussion sections, benthic units with FADs are referred to as FP units ( $\underline{F}$ AD  $\underline{P}$ resent), and benthic units without FADs are referred to as FN units ( $\underline{F}$ AD  $\underline{N}$ ot Present). Benthic units with holes (large or small) are referred to as HP units ( $\underline{H}$ oles  $\underline{P}$ resent), and benthic units without holes are referred to as HN units ( $\underline{H}$ oles  $\underline{N}$ ot Present).

In order to study all possible combinations of hole size and vertical profile, the following six construction designs were tested (Fig. 1):

- (a) Control units (no holes); FAD not present;
- (b) Benthic units with six small diameter holes; FAD not present;
- (c) Benthic units with six large diameter holes; FAD not present;
- (d) Control units (no holes); FAD present;
- (e) Benthic units with six small diameter holes; FAD present; and
- (f) Benthic units with six large diameter holes; FAD present.

The experimental units were deployed on 25 April 1994 in 14 m of water. Five replicates of each reef design were deployed, giving a total of six designs  $\times$  five replicates = 30 total reef units. The units were deployed in a single straight line in a randomized block design to control for possible temporal and location effects (Fig. 2). Each reef unit was spaced approximately 30 m from its neighboring unit(s), and was secured to a screw anchor to prevent movement of the units by strong water currents.



Figure 2. Experimental design. Five randomized blocks, containing each of the six artificial reef designs, were deployed in a single line. The distance between consecutive reef units was 30 m. The double arrow denotes the concrete block anchoring the end line.

All benthic units were attached to each other at the base with a connecting line. Plastic end lines extended approximately 30 m from the experimental units on both ends of the line of reefs (Fig. 2). These lines were anchored by a concrete cinder block and were designed to help divers more easily locate the first experimental unit to be sampled. End lines were also used as sites for control censuses. Sampling of the units always began at one end of the line of experimental units and was completed at the opposite end of the line of units. Divers swam with the tide to lessen travel time between the units. The end at which censusing began was therefore determined on each sample day with regard to tidal conditions.

The experimental units were censused eight times from 24 May 1994 to 4 November 1994 (Table 1). Sample days 6 and 7 occurred on consecutive days but were determined to be statistically independent. Censusing was performed following a variation of the stationary sampling method of Bohnsack and Bannerot (1986). During each census one observer (GTK) followed the connecting line until an experimental unit was visible. The observer then recorded the species present, the number of individuals representing each species, and the depth, time, and type of unit on underwater paper. Fishes censused on units with attached FADs were classified as associated with the benthic unit or associated with the FAD; on FN units all individuals were classified as benthic. This practice led to the classification of some species that could be considered pelagic (e.g., *Decapterus punctatus*) as benthic. All fishes present on FN units, whether benthic or pelagic, were assumed to have been recruited by the benthic unit. Equal numbers of benthic species and individuals would be expected to have been recruited by the benthic units on FP units (null hypothesis). Any differences in numbers of species and individuals between FP and FN units were hypothesized to be due to effects of the FAD.

In some cases schools of *D. punctatus* and/or *Stenotomus chrysops* were too numerous to count; in these instances estimates to the nearest multiple of ten were recorded. Minimum, maximum, and average total lengths were estimated for each species using a marked measuring board for reference. The spatial positioning of individuals in regard to the experimental unit was also documented.

Table 1. Sample numbers, corresponding dates, and water temperatures recorded during each sample.

Sample	Date (1994)	Days after deployment	Temperature (oC)
deployment	25 April	*	*
1	24 May	29	21
2	2 June	38	24
3	22 June	59	25
4	11 July	78	26
5	1 August	99	25
6	26 August	123	27
7	27 August	124	28
8	4 November	193	20

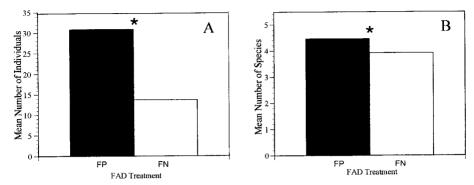


Figure 3. (A) Mean number of individuals and (B) mean number of species for all sample days combined by FAD treatment. The asterisk (\*) denotes a significant difference (P < 0.05) between means.

For example, individuals may have been noted as being on the FAD, inside or outside of the benthic unit, or upcurrent or downcurrent from the unit or FAD. Fishes that followed divers during censusing were recorded only at the unit where they were first observed. All 30 units and two additional control sites were censused on each sampling date. Two dives were required on each date to census all units.

The crested blenny (*Hypleurochilus geminatus*) was observed on most experimental benthic units throughout the study, but was difficult to census due to its small size, cryptic coloration, and cryptic behavior. *Hypleurochilus geminatus* was excluded from analyses because censuses of their abundances were considered inaccurate.

Statistical comparisons were performed using parametric Analysis of Variance (anova) procedures on rank-transformed data (Conover, 1980; Conover and Iman, 1981; Zar, 1984). All anova

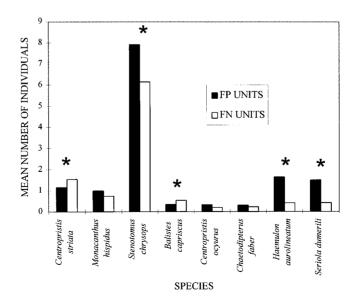


Figure 4. Mean number of individuals, by species, for all sample days combined by FAD treatment. The species listed were the eight most abundant species observed during the study. The asterisk (\*) denotes a significant difference (P < 0.05) between means.

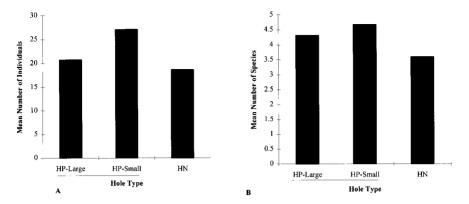


Figure 5. (A) Mean number of individuals and (B) mean number of species for all sample days combined by hole size treatment. Means that are not significantly different are underlined.

comparisons were performed using the Statistical Analysis System (SAS), available from SAS Institute Inc., Cary, NC, USA.

#### RESULTS

Vertical Profile.—Mean number of benthic individuals per experimental unit was significantly greater on FP units than on FN units (4-way anova, P < 0.0001; Fig. 3A). Mean number of benthic species per unit was also significantly greater on FP units than on FN units (4-way anova, P = 0.0163; Fig. 3B). In analyses of individual species, three species were significantly more abundant on FP units than on FN units: *Seriola dumerili* (3-way anova, P = 0.0462), *Stenotomus chrysops* (3-way anova, P = 0.0006), and *Haemulon aurolineatum* (3-way anova, P < 0.0001) (Fig. 4). *Centropristis ocyurus* (3-way anova, P = 0.0550) was nearly significantly more abundant on FP units than on FN units. Abundances of *Monacanthus hispidus* and *Chaetodipterus faber* were nominally greater on FP

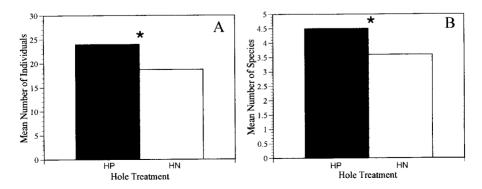


Figure 6. (A) Mean number of individuals and (B) mean number of species for all sample days combined by hole presence treatment. The asterisk (\*) denotes a significant difference (p<.05) between means.

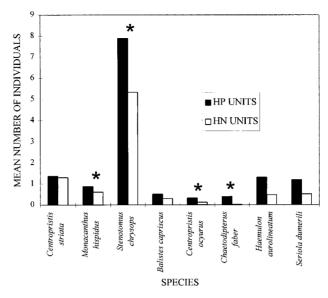


Figure 7. Mean number of individuals, by species, for all sample days combined by hole presence treatment. The asterisk (\*) denotes a significant difference (P < 0.05) between means.

units than on FN units for all sample days combined. *Centropristis striata* (3-way anova, P = 0.0157) and *Balistes capriscus* (3-way anova, P = 0.0408) were significantly more abundant on FN units than on FP units.

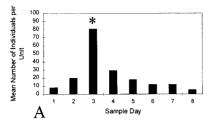
Hole Diameter.—Hole diameter was found to have no significant effect on estimated average lengths of fishes attracted to the experimental units (3-way anova, P > 0.05 for all cases). In analyses of abundance, mean number of benthic individuals was greatest on HP units with small diameter holes and least on HN units for all sample days combined (Fig. 5A). Mean numbers on HP units with small diameter holes and HP units with large diameter holes were significantly greater than mean number on HN units but not significantly different from each other (4-way anova, P < 0.0001; Tukey test).

Mean number of benthic species was also greatest on HP units with small diameter holes and least on HN units for all sample days combined (Fig. 5B). Mean number of benthic species on HP units with small diameter holes and mean number on HP units with large diameter holes were significantly greater than mean number on HN units but not significantly different from each other (4-way anova, P < 0.0001; Tukey test).

Greatest mean abundance varied by species between HP units with large diameter holes and HP units with small diameter holes. *Monacanthus hispidus, C. ocyurus,* and *C. faber* were most abundant on HP units with large diameter holes for all sample days combined. Mean abundance of *C. faber* was significantly greater on HP units with large diameter holes than on HP units with small diameter holes and on HN units (4-way anova, P < 0.0001; Tukey test). Mean abundance of *M. hispidus* and *C. ocyurus* were significantly greater on HP units with large diameter holes than on HN units, but were not significantly greater than mean abundances on HP units with small diameter holes (Tukey test). *Centropristis striata, S. chrysops, B. capriscus, H. aurolineatum,* and *S. dumerili* were most abundant on HP units with small diameter holes.

Table 2. Abundance and frequency of fishes observed on reef units. Reef associations includes those with benthic units (B), with the FAD (F) or with both (BF). Life stages include juveniles (J) and adults (A).

Family	Number	Percent	Reef	Life	
Species	observed	total	frequency	association	Stage
Dasyatidae			- 1 - 1		
Dasyatis sp.	2	0.04	0.56	В	J
Synodontidae	_			_	-
Synodus sp.	4	0.07	1.67	В	
Gadidae	•	0.07	1.07	2	
Urophycis sp.	3	0.05	1.25	В	Α
Triglidae	5	0.05	1.23	Б	11
Prionotus sp.	2	0.04	0.83	В	
Serranidae	-	0.04	0.03	Ь	
Centropristis ocyurus	63	1.11	21.67	В	JA
Centropristis striata	324	5.7	81.66	В	JA
Diplectrum formosum	104	1.83	33.75	В	JA
Mycteroperca microlepis	2	0.04	0.83	В	A
Mycteroperca phenax	4	0.04	1.67	В	A
Echeneididae	0.02		BF	ь	
	0.02	0.42	БΓ		
Carangidae	60	1.2	6.67	DE	
Caranx sp.	68	1.2	6.67	BF	A
Decapterus punctatus	2,197	38.65	35.42	BF	JA
Seriola dumerili	233	4.1	13.75	BF	A
Seriola fasciata	1	0.02	0.42	BF	A
Seriola zonata	44	0.77	5.42	BF	A
Lutjanidae					
Lutjanus sp.	7	0.12	2.92	В	
Haemulidae					
Haemulon aurolineatum	247	4.35	17.92	В	
Orthopristis chrysoptera	1	0.02	0.42	В	
Sparidae					
Archosargus probatocephalus	32	0.56	10	В	JA
Calamus leucosteus	1	0.02	0.42	В	A
Diplodus holbrooki	1	0.02	0.42	В	J
Lagodon rhomboides	9	0.16	3.33	В	J
Stenotomus chrysops	1,688	29.7	72.08	В	
Sciaenidae					
Equetus lanceolatus	2	0.04	0.42	В	
Equetus umbrosus	3	0.05	1.25	В	
Mullidae					
Mullus auratus	1	0.02	0.42	В	
Upeneus parvus	49	0.86	9.58	В	
Ephippidae					
Chaetodipterus faber	73	1.28	21.25	BF	J
Sphyraenidae					
Sphyraena barracuda	2	0.04	0.83	В	J
Labridae					
Halichoeres bivittata	9	0.16	3.75	В	
Blennidae				_	
Hypleurochilus geminatus	*	*	*	В	JA
Balistidae				Ь	371
Balistes capriscus	109	1.92	26.66	В	J
Monacanthus hispidus	315	5.54	76.25	BF	J
Diodontidae	313	3.34	10.23	DI.	
Chilomycterus schoepfi	3	0.05	1.25	В	J
Chilomycierus schoepji	3	0.03	1.43	ь	J



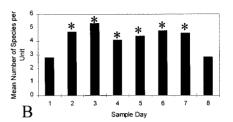


Figure 8. (A) Mean number of individuals and (B) mean number of species per unit per sample day. Abundances on sample days labeled with an asterisk (\*) are significantly greater (P < 0.05) than abundances on unlabeled sample days.

Hole Presence.—Data from large diameter and small diameter units were combined to determine whether the presence of holes, regardless of diameter, significantly affected individual finfish abundance and species richness. Mean number of benthic fishes was significantly greater on HP units than on HN units (4-way anova, P < 0.0001; Fig. 6A). Mean number of benthic species was also significantly greater on HP units than on HN units (4-way anova, P < 0.0001; Fig. 6B).

Four species were significantly more abundant on HP units than on HN units (Fig. 7): *S. chrysops* (3-way anova, P < 0.0001), *M. hispidus* (3-way anova, P = 0.0041), *C. ocyurus* (3-way anova, P = 0.0055), and *C. faber* (3-way anova, P < 0.0001). Mean abundances of *C. striata*, *B. capriscus*, *H. aurolineatum*, and *Seriola dumerili* were nominally greater on HP units than on HN units.

Species Assemblages.—Sixteen families of fishes and 33 species (5604 individuals) were identified on the six artificial reef designs during the course of the study (Table 2). The six dominant species, combined over the entire sample period and ranked by individual abundance, were round scad (*D. punctatus*), scup (*S. chrysops*), black sea bass (*C.* 

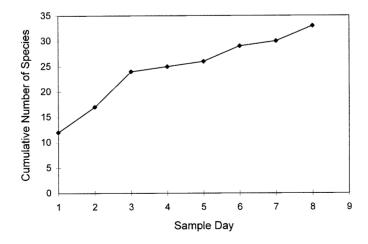


Figure 9. Cumulative number of species observed per sample.

Day number	Mean number (± 1 s.d.)	Streamers buoyant	Streamers not buoyant
29	$2.90 \pm 4.33$	*	<u> </u>
38	$6.77 \pm 6.43$	*	
59	$53.40 \pm 62.36$	*	
78	$8.33 \pm 27.77$	*	
99	$0.00 \pm 0.00$		*
123	$0.67 \pm 2.86$		*
124	$0.17 \pm 0.75$		*
193	$1.00 \pm 5.48$		*

Table 3. Mean numbers of *Decapterus punctatus* by sample day, with regard to buoyancy of FAD streamers.

*striata*), planehead filefish (*M. hispidus*), tomtate (*H. aurolineatum*), and greater amberjack (*S. dumerili*). Fourteen species were represented by three or fewer individuals and occurred on less than 1% of the censused reefs.

Mean number of finfish individuals on each reef varied by sample day (Fig. 8A). Mean number of fishes was significantly greater on day 59 than on any other sample day (1-way anova, P < 0.0001).

Mean number of species on each reef also varied by sample day, although increasing and decreasing trends were not as evident (Fig. 8B). Mean numbers of species on days 38, 59, 78, 99, 123, and 124 were significantly greater than mean numbers on days 29 and 193 (1-way anova, P < 0.0001; Tukey test). The presence of individual species was affected by seasonality. Previously unobserved species were censused on every sample day (Fig. 9).

Temperature had a significant effect on mean individual abundance and mean number of species per experimental unit for all sample days combined (4-way anova, P < 0.0001). Temperature had no significant interaction with FAD presence or hole diameter in analyses of individual abundance and number of species per unit (4-way anova, P > 0.05).

Day number also had a significant effect on mean individual abundance and mean number of species per experimental unit for all sample days combined (4-way anova, P < 0.0001). Day number had no significant interaction with FAD presence or hole diameter in analyses of individual abundance and number of species per unit (4-way anova, P > 0.05).

A drop in the number of FAD-associated fishes, especially round scad (D. punctatus), occurred with time (Table 3). Mean numbers of D. punctatus on days 99, 123, 124, and 193 were significantly less than mean numbers on days 38, 59, and 78 (4-way anova, P < 0.0001, Tukey test).

REEF DESIGN.—No fishes were observed to orient to the connecting lines attached to adjacent units. The connecting lines were nearly completely covered by sand on most census dates. By day 193 the connecting lines were buried several centimeters in the sand and were difficult to locate.

No movement of the experimental units due to storm surges occurred. All 30 experimental units remained upright and in their original position throughout the study. Scouring caused most of the units to subside 12–15 cm into the sand by day 193.

The FADs functioned well over the first four sample days (Table 3). The floats kept the main line of the FAD vertical in the water column, and the plastic streamers were stretched out in the water current. Very slight currents were enough to keep the streamers perpen-

dicular to the main line. By day 99 the FADs became heavily fouled with barnacles. The float was still buoyant enough to keep the main line of the FAD hanging vertically in the water column, but the streamers sagged almost straight down from the weight of the barnacles. Only in conditions of strong current would the streamers move at an angle to the main line.

#### DISCUSSION

The significant differences between the mean numbers of benthic fishes aggregated to FP units and to FN units support the hypothesis that benthic finfish species richness and individual abundances are positively affected by an increase in artificial reef vertical profile. Several factors may have contributed to the increased concentration of benthic finfishes on the FP units. One possibility is that the fishes composing the benthic communities on the experimental units were somehow affected by the pelagic community attracted to the FP units. For example, fishes associated with the FAD and fouling organisms on the FAD may indirectly affect the benthic fish community by enhancing the benthic productivity of the area below the FAD. Numerous studies have shown that fishes can be a source of mineral and nutrient input to the benthic community, and can attract and enhance the growth of benthic organisms (see, for example, Bray et al., 1981; Geesey et al., 1984; Meyer and Schultz, 1985a Meyer and Shultz, 1985b; Hamner et al., 1988; Rothans and Miller, 1991). FAD-associated fishes could affect benthic productivity by increasing energy flow to the benthos. Fecal materials, uneaten food particles, and occasional fish carcasses due to natural mortality are produced by pelagic fishes (Buckley, 1989; Rountree, 1990). Pseudofeces, feces, and other organic litter is produced by the fouling community (Rountree, 1990). These materials may fall as organic rain to the benthos below the FAD, increasing nutrient supply to the benthos and thus increasing benthic productivity. An increased benthic fauna could attract and support greater numbers of benthic-feeding fishes, which could in turn support more fishes that feed on benthicfeeding fishes. However, any hypothesis of increased benthic productivity must allow time for trophic transfer processes to take place. A significant increase in benthic fish abundance over a short time period would require other causative factors.

A second factor possibly contributing to the greater mean numbers of benthic fishes on FP units is that piscivorous benthic fishes were feeding on small pelagic fishes associated with the FAD. In this case benthic fishes would be more likely to associate with the FP units than with FN units because of the increased availability of prey on the FP units.

The pelagic fishes associated with the FADs may have had no causative effect on the increased numbers of benthic fishes associated with FP units. Mean numbers of pelagic fishes associated with the FADs dropped significantly after day 78, when the FAD streamers lost their buoyancy. If the presence of the pelagic fish community was somehow causing an increase in the number of benthic fishes on the FP units, then mean numbers of benthic fishes would be expected to decrease and become equal to mean numbers on FN units as the pelagic fish community disappeared. However, the mean number of individuals on the benthic units was significantly greater on FP units than on FN units on day 123 and almost significantly greater on day 124, even though the numbers of pelagic fishes associated with the FADs had greatly decreased by this time. These results suggest that other factors were involved in causing the increased numbers of benthic fishes on the FP units.

The FAD fouling community, present after the drop in FAD-associated fish abundance, may have continued to positively affect mean numbers of benthic finfish species and individuals. Other causes may have been related to the design of the FP units. For example, benthic fishes may have been better able to visually cue to the FP units because of their increased vertical profile. FP units may have been visible to fishes from farther away than FN units, causing more fish to be attracted to FP units. Secondly, Fee (1985) suggested that fishes may be attracted to artificial reefs by low frequency sounds emitted by FADs. The lateral line of fishes functions as a low frequency sound detector (Tavolga, 1971). Many species of marine fishes have been demonstrated to respond to low frequency sounds (see, for example, Fine and Lenhardt, 1983; Haymes and Patrick, 1986; Takemura et al., 1988). Because the water off the coast of South Carolina is sometimes murky from current-carried particulate matter, it is possible that fishes may depend on sound to orient themselves to reef areas. The emittance of low frequency sounds from the FADs of FP units may therefore have contributed to the greater mean numbers of benthic fish species and individuals on FP units.

HOLE DIAMETER.—One attractive feature of artificial reefs is the shelter they offer. Holes offer shelter from predators and water currents (Laufle and Pauley, 1985; Hixon and Beets, 1989; present study), and can have an effect on the types and number of species and individuals present on artificial reefs (Hixon and Beets, 1989). Units with no holes (HN units) and HP units with small or large diameter holes offer different amounts of shelter to reef fishes. During the study, fishes such as black sea bass (*C. striata*), spadefish (*C. faber*), gray triggerfish (*B. capriscus*), and a species of hake (*Urophycis* sp.) were often observed inside the units equipped with holes. On one occasion, a *Urophycis* sp. individual remained inside a benthic unit despite repeated attempts by a diver (GTK) to remove it for identification.

The lengths of fishes associated with the benthic units were not significantly related to the hole diameter of the units. This result contradicts the results of a previous study of hole size/fish length interactions (Hixon and Beets, 1989), which reported a general positive correlation between hole size and fish size. In explanation of this correlation, Hixon and Beets (1989) suggested that an increase in the number of large holes caused an increase in the abundance of large piscivorous fishes, which in turn caused a decrease in the local abundance of small prey fishes. We believe that fish sizes were never significantly related to hole diameter in this study because of the design of the benthic structures. Total surface area of holes in our study was 127 cm<sup>2</sup> for small holes and 507 cm<sup>2</sup> for large holes. We suggest that each of these hole sizes were, in effect, large holes. On several instances large fishes (length >20 cm) were observed inside HP units with small diameter holes. GTK once observed a 30 cm (total length) gray triggerfish (B. capriscus) wriggle through a small hole at the approach of divers. Although B. capriscus is not a piscivorous fish, the ability of a 30-cm fish to enter into the benthic unit through the 12.7 cm diameter hole certainly suggests that other large piscivorous fishes could perform the same feat. If the "small" holes used in this study were, in effect, "large" holes, one would not expect to find differences in mean fish sizes between HP units containing small and large diameter holes. These results suggest that a limiting diameter exists for small holes to effectively attract small fishes. Further studies using a greater gradient of hole diameters could help to define this size and are recommended.

The minimal differences between the numbers of species and individuals attracted to each type of HP unit (HP-large vs HP small) did not support the hypothesis that hole

diameter would affect the mean number of finfish species and individuals attracted to artificial reefs. These results were most likely due to the fact that the small diameter holes in this study were too large to effectively serve as shelter for small fishes.

Hole Presence.—The significant differences between mean numbers of benthic finfishes aggregated to HP units (Holes Present) and HN units (Holes Absent) support the hypothesis that the addition of holes to an artificial reef can increase the mean numbers of finfish species and individuals present on that reef. One possibility explaining the smaller numbers of species and individuals on HN units may have been that HN units had lower juvenile and adult recruitment rates than either type of HP unit. Fishes originally attracted to HN units may have found the units unsuitable as habitat due to lack of shelter and continued to search for more suitable habitat. Predation rates may also have been higher on HN units. HN units offered less shelter and therefore less protection from predators than HP units.

Species Assemblages and Seasonality.—The 16 families and 33 species of fishes identified on the experimental units during the course of the study is comparable to the number of families and species observed on artificial and/or natural reefs in surveys performed in the South Atlantic Bight (Rountree, 1990; Potts and Hurlbert, 1994). The temporal occurrence of fish species observed during the study was most likely affected by seasonality. Previous studies have shown that high seasonal variation in the fish species present exists at many natural and artificial reefs (Molles, 1978; Chandler et al., 1985; Lindquist et al., 1985; Stephan and Lindquist, 1989; Naito, 1991). Ogren (1974) reported that changes in temperature can affect seasonal variation in finfish abundance on artificial reefs. Temperature has been reported to cue seasonal movements in several of the finfish species present in this study. As water temperatures cooled seasonally, D. punctatus became less abundant on the experimental units. This decrease in abundance of *D. punctatus* may have been due to a seasonal offshore migration as reported by Hales (1987). Other seasonal migrations may also have affected daily abundance. No H. aurolineatum were observed on day 193 (4 November), although individuals were present on the five previous sample days. H. aurolineatum has been reported to migrate offshore during the fall and winter months (Stephan and Lindquist, 1989). A seasonal movement of C. striata occurs annually during the fall as juveniles of the species move offshore from estuaries and settle on coastal reefs and natural hard-bottom habitat (Wenner et al., 1986). This seasonal movement was evident on day 193, when many 10-15 cm individuals, previously in low abundance, were observed on the benthic units.

Mean numbers of finfish species and individuals per experimental unit varied seasonally. Fewer species and individuals were observed on days 29 and 193 than on any other sample days. These low numbers of species and individuals coincided with temperature minimums for the study period, and may have been due to seasonal migrations of certain finfish species, as discussed above.

REEF DESIGN.—An important factor in the prefabrication and deployment of artificial reefs is the design of the reef units. Reef units that are not properly weighted or designed may be moved by strong bottom currents that occur during stormy weather (M. Bell, pers. comm.). Observations suggest that the general design of the benthic units used in this study is acceptable for use in the prefabrication of artificial reefs to be deployed off the coast of South Carolina, although the units were not subjected to the severe storms that occasionally occur. Concerns regarding the movement of the benthic units during the study were unfounded. Each of the thirty units remained upright and in its original posi-

tion throughout the sample period. By October 1994, scouring had caused most of the benthic units to subside 12–15 cm into the sand bottom. This subsidence presumably increased the stability of each unit by lessening the chance of movement by strong bottom currents.

All censused species were at some time observed on units lacking FADs. The lack of species associated only with the FAD indicates that the benthic units by themselves were effective in attracting pelagic and/or semi-pelagic species to the general reef area. FADs were not critical to the attraction of any species observed during the study.

The FAD design was not as successful as the benthic unit design. FADs of the design used in this study are most functional in fish attraction when the streamers are extended and flowing in the current. Many fish use the streamers as protection, both visually and physically, from predators (Randall and Randall, 1960; Hunter, 1968; Chandler et al., 1985; Rountree, 1989). When streamers become fouled and lose their buoyancy, most of their protective area is lost. At this point FADs presumably become less attractive to fishes that would normally swim in or near the streamers. FADs are used mainly to attract baitfishes such as round scad (Klima and Wickham, 1971; Feigenbaum et al., 1989; Stephan and Lindquist, 1989; Rountree, 1990). The FAD-associated baitfishes are effective in attracting and concentrating certain commercially and recreationally important pelagic gamefish species into the general area (Klima and Wickham, 1971; Brock, 1985; Pollard and Matthews, 1985; Workman et al., 1985; Buckley et al., 1989). When an FAD loses its ability to attract baitfishes, its attractiveness to piscivorous pelagic fishes may be reduced. By day 99, the FAD streamers had become heavily fouled by barnacles, causing the streamers to hang down, parallel to the main line. A significant drop in the numbers of FAD-associated baitfish, especially round scad (D. punctatus), occurred concurrently with the fouling of the FAD streamers. It is not known whether this drop in *D. punctatus* was caused entirely by the fouling and subsequent sinking of the FAD streamers or whether the drop simply occurred concurrently with the fouling of the streamers and was caused in part or entirely by other factors. However, this significant reduction in baitfish individuals suggests a related loss of predatory fishes such as S. maculatus and S. cavalla, which in turn implies a weakness in the ability of the FAD to attract these species. An improved FAD design would put to use materials that could maintain buoyancy in the presence of heavy fouling. To date most midwater FAD designs have proved unsuccessful in lasting for extended time periods (Matsumoto et al., 1981; Chandler et al., 1985; Pollard and Matthews, 1985; Buckley, 1989; Wilkins and Goodwin, 1989).

The location of the study site may have affected the faunal composition of the colonizers and the rate at which colonization took place. The proximity of an artificial reef to natural reefs, other artificial reefs, or hard-bottom areas is important in the establishment of community structure on that artificial reef (de Sylva, 1982; Carter et al., 1985; Matthews, 1985; Wendt et al., 1989). The importance of location is stressed in several studies that suggest that location, not reef design, is the greatest factor affecting both fish community development on an artificial reef and the rate at which that development occurs (Matsumoto et al., 1981; Alevizon et al., 1985; Workman et al., 1985). For example, Workman et al. (1985) reported that species diversity and fish abundance were greater on artificial structures located nearer natural reefs than on those located farther away.

All experimental units in this study were roughly equidistant from any given recruitment source. The nearest known recruitment source was Capers Artificial Reef (CAR), one of the largest and most heavily fished artificial reefs off the coast of South Carolina

(Low and Waltz, 1991). The experimental units used in this study were positioned approximately 0.8 km (0.5 nm) from CAR. Although the ranges at which different species of fish may be attracted from one reef to another are not well known, fishes were most likely attracted to the experimental units from CAR and possibly from uncharted hard-bottom areas in the vicinity of the study area. Some fishes observed during the study probably moved from coastal estuarine areas to the experimental units as local water temperatures declined. Many of the black sea bass (*C. striata*) censused on day 193 are believed to have been recruits from coastal estuaries (*C. Wenner*, pers. comm.).

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### LITERATURE CITED

- Alevizon, W. S., J. C. Gorham, R. Richardson, and S. A. McCarthy. 1985. Use of man-made reefs to concentrate snapper (Lutjanidae) and grunts (Haemulidae) in Bahamian waters. Bull. Mar. Sci. 37: 3–10.
- Beets, J. 1989. Experimental evaluation of fish recruitment to combinations of fish aggregating devices and benthic artificial reefs. Bull. Mar. Sci. 44: 973–983.
- Bell, M., C. J. Moore, and S. W. Murphey. 1989. Utilization of manufactured reef structures in South Carolina's Marine Artificial Reef Program. Bull. Mar. Sci. 44: 818–830.
- Bohnsack, J. A. and S. Bannerot. 1986. A stationary visual technique for quantitatively assessing community structure of coral reef fishes. NOAA Tech. Rep. NMFS 41.
- , D. E. Harper, D. B. McClellan, and M. Hulsbeck. 1994. Effects of reef size on colonization and assemblage structure of fishes at artificial reefs off southeastern Florida, U.S.A. Bull. Mar. Sci. 55: 796-823.
- \_\_\_\_\_\_, and D. L. Sutherland. 1985. Artificial reef research: a review with recommendations for future priorities. Bull. Mar. Sci. 37: 11–39.
- Bray, R. N., A. C. Miller, and G. G. Geesey. 1981. The fish connection: a trophic link between planktonic and rocky reef communities? Science 214: 204–205.
- Brock, R. E. 1985. Preliminary study of the feeding habits of pelagic fish around Hawaiian fish aggregation devices (FADs) or can FADs enhance local fisheries productivity? Bull. Mar. Sci. 37: 40–49.
- Buckley, R. M. 1982. Marine habitat enhancement and urban recreational fishing in Washington. Mar. Fish. Rev. 44: 28–37.
- \_\_\_\_\_. 1989. Habitat alterations as a basis for enhancing marine fisheries. Cal. Coop. Ocean. Fish. Invest. Rep. 30: 40–45.
- and G. J. Hueckel. 1985. Biological processes and ecological development on an artificial reef in Puget Sound, Washington. Bull. Mar. Sci. 37: 50–69.

- \_\_\_\_\_\_, D. G. Itano, and T. W. Buckley. 1989. Fish aggregation device (FAD) enhancement of offshore fisheries in American Samoa. Bull. Mar. Sci. 44: 942–949.
- Carter, J. W., W. N. Jesse, M. S. Foster, and A. L. Carpenter. 1985. Management of artificial reefs designed to support natural communities. Bull. Mar. Sci. 37: 114–128.
- Chandler, C.R., R.M. Sanders, Jr., and A.M. Landry, Jr. 1985. Effects of three substrate variables on two artificial reef fish communities. Bull. Mar. Sci. 37: 129–142.
- Conover, W. J. 1980. Practical nonparametric statistics, 2nd ed. John Wiley and Sons, Inc., New York.
- \_\_\_\_\_ and R. L. Iman. 1981. Rank transformations as a bridge between parametric and nonparametric statistics. Amer. Statistician 3: 124–133.
- Davis, G. E. 1985. Artificial structures to mitigate marina construction impacts on spiny lobster, *Panulirus argus*. Bull. Mar. Sci. 37: 151–156.
- de Sylva, D. P. 1982. Potential for increasing artisanal fisheries production from floating artificial habitats in the Caribbean. Proc. 34th Ann. Gulf .Carib. Fish. Inst., November 1981. No. 34: 156-167.
- Dewees, C. M. and D. W. Gotshall. 1974. An experimental artificial reef in Humboldt Bay, California. Calif. Fish and Game 60: 109-127.
- Duedall, I. W., D. R. Kester, P. K. Park, and B. H. Ketchum, eds. 1985. Wastes in the ocean. *In* Energy wastes in the ocean. Vol. 4: 717–739.
- Fagerstrom, J.A. 1987. The evolution of reef communities. John Wiley and Sons, Inc., New York. Fee, R. 1985. Reefs and FADs: new tools for bigger catches? Nat. Fish. 66: 14–15.
- Feigenbaum, D. M., A. Friedlander, and M. Bushing. 1989. Determination of the feasibility of fish attracting devices for enhancing fisheries in Puerto Rico. Bull. Mar. Sci. 44: 950–959.
- Fine, M. L. and M. L. Lenhardt. 1983. Shallow-water propagation of the toadfish mating call. Comp. Biochem. Physiol., A. 76A(2): 225–231.
- Geesey, G. G., G. V. Alexander, R. N. Bray, and A. C. Miller. 1984. Fish fecal pellets are a source of minerals for inshore reef communities. Mar. Ecol. Prog. Ser. 15: 19–25.
- Hales, L. Stanton, Jr. 1987. Distribution, abundance, reproduction, food habits, age, and growth of round scad, *Decapterus punctatus*, in the South Atlantic Bight. Fish. Bull., U.S. 85: 251–268.
- Hammond, D. L., D. O. Myatt, and D. M. Cupka. 1977. Evaluation of midwater structures as a potential tool in the management of the fisheries resources on South Carolina's artificial fishing reefs. So. Car. Mar. Res. Center Tech. Rep. 15. 19 p.
- Hamner, W. M., M. S. Jones, J. H. Carleton, I. R. Hauri, and D. McB. Williams. 1988. Zooplankton, planktivorous fish, and water currents on a windward reef face: Great Barrier Reef, Australia. Bull. Mar. Sci. 42: 459–479.
- Haymes, G. T. and P. H. Patrick. 1986. Exclusion of adult alewife, *Alosa pseudoharengus*, using low frequency sound for application at water intakes. Can. J. Fish. Aquat. Sci. 43: 855–862.
- Hixon, M. A. and J. P. Beets. 1989. Shelter characteristics and Caribbean fish assemblages: experiments with artificial reefs. Bull. Mar. Sci. 44: 666–680.
- Hueckel, G. J., R. M. Buckley, and B. L. Benson. 1989. Mitigating rocky habitat loss using artificial reefs. Bull. Mar. Sci. 44: 913–922.
- Hunter, J. R. 1968. Fishes beneath flotsam. Sea Frontiers 14: 280–288.
- Klima, E. F. and D. A. Wickham. 1971. Association of coastal pelagic fishes with artificial structures. Trans. Amer. Fish. Soc. 100: 86–99.
- Laufle, J. C. and G. B. Pauley. 1985. Fish colonization and materials comparisons on a Puget Sound artificial reef. Bull. Mar. Sci. 37: 227–243.
- Lindquist, D. G., M. V. Ogburn, W. B. Stanley, H. L. Troutman, and S. M. Pereira. 1985. Fish utilization patterns on temperate rubble-mound jetties in North Carolina. Bull. Mar. Sci. 37: 244–251.
- Low, R. A., Jr. and C. W. Waltz. 1991. Seasonal utilization and movement of black sea bass on a South Carolina artificial reef. N. Am. J. Fish. Manage. 11: 131–138.

- Matsumoto, W. M., T. K. Kazama, and D. C. Aasted. 1981. Anchored fish aggregation devices in Hawaiian waters. Mar. Fish. Rev. 43: 1–13.
- Matthews, K. R. 1985. Species similarity and movement of fishes on natural and artificial reefs in Monterey Bay, California. Bull. Mar. Sci. 37: 252–270.
- \_\_\_\_\_. 1990. A comparative study of habitat use by young-of-the-year, subadult, and adult rockfishes on four habitat types in central Puget Sound. Fish. Bull., U.S. 88: 223–239.
- Meyer, J. L. and E. T. Schultz. 1985a. Migrating haemulid fishes as a source of nutrients and organic matter on coral reefs. Limnol. Oceanogr. 30: 146–156.
- and \_\_\_\_\_\_. 1985b. Tissue condition and growth rate of corals associated with schooling fish. Limnol. Oceanogr. 30: 157–166.
- Molles, M. C., Jr. 1978. Fish species diversity on model and natural reef patches: experimental insular biogeography. Ecol. Monogr. 48: 289–305.
- Mottet, M. G. 1985. Enhancement of the marine environment for fisheries and aquaculture in Japan. Pages 54–58 in F. D'itri, ed. Artificial reefs-marine and freshwater applications. Lewis Publishers, Inc., Chelsea, Michigan. 589 p.
- Myatt, D. O. 1981. Planning considerations for reef construction. Pages 41–49 *in* D. Y. Aska, ed. Artificial Reefs: Proc. Conf. 13–15 September 1979, Daytona Beach, Florida.
- Naito, B. G. 1991. A biological survey of an artificial reef at French Creek, British Columbia. Can. Manuscr. Rep. Fish. Aquat. Sci. 2100. 37 p.
- Ogawa, Y. 1967. Experiments on the attractiveness of artificial reefs for marine fishes. VII. Attraction of fishes to the various sizes of model reefs. Bull. Jap. Soc. Sci. Fish. 33: 801–811.
- Ogren, L. H. 1974. Midwater structures for enhancing recreational fishing. Pages 65–67 *in* Proc. Artificial Reef Conference, Houston, Texas.
- Pollard, D. A. and J. Matthews. 1985. Experience in the construction and siting of artificial reefs and fish aggregation devices in Australian waters, with notes on and a bibliography of Australian studies. Bull. Mar. Sci. 37: 299–304.
- Potts, T. A. and A. W. Hurlbert. 1994. Structural influences of artificial and natural habitats on fish aggregations in Onslow Bay, North Carolina. Bull. Mar. Sci. 55: 609–622.
- Randall, J. E. 1963. An analysis of the fish populations of artificial and natural reefs in the Virgin Islands. Carib. J. Sci. 3: 31–47.
- and H. A. Randall. 1960. Examples of mimicry and protective resemblance in tropical marine fishes. Bull. Mar. Sci. 10: 444–480.
- Robertson, D. R. and J. M. Sheldon. 1979. Competitive interactions and the availability of sleeping sites for a diurnal coral reef fish. J. Exp. Mar. Biol. Ecol. 40: 285–298.
- Rothans, T. C. and A. C. Miller. 1991. A link between biologically imported particulate organic nutrients and the detritus food web in reef communities. Mar. Biol. 110: 145–150.
- Rountree, R. A. 1987. Ecology of the association of fishes with fish aggregation devices (FADs): M.S. Thesis. College of Charleston, South Carolina. 176 p.
- . 1989. Association of fishes with fish aggregation devices: Effects of structure size on fish abundance. Bull. Mar. Sci. 44: 960–972.
- \_\_\_\_\_. 1990. Community structure of fishes attracted to shallow-water fish aggregation devices off South Carolina, U.S.A. Environ. Biol. Fish. 29: 241–262.
- Seaman, W., Jr., R. M. Buckley, and J. J. Polovina. 1989. Advances in knowledge and priorities for research, technology and management related to artificial aquatic habitats. Bull. Mar. Sci. 44: 527–532.
- Sheehy, D. H. 1982. The use of designed and prefabricated artificial reefs in the United States. Mar. Fish. Rev. 44: 4–15.
- Shulman, M. J. 1984. Resource limitation and recruitment patterns in a coral reef fish assemblage. J. Exp. Mar. Biol. Ecol. 74: 85–109.
- Spanier, E., M. Tom, and S. Pisanty. 1985. Enhancement of fish recruitment by artificial enrichment of man-made reefs in the southeastern Mediterranean. Bull. Mar. Sci. 37: 356–363.

- Stephan, C. D. and D. G. Lindquist. 1989. A comparative analysis of the fish assemblages associated with old and new shipwrecks and fish aggregation devices in Onslow Bay, North Carolina. Bull. Mar. Sci. 44: 698–717.
- Stone, R. B. 1982. Artificial reefs: toward a new era in fisheries enhancement? Mar. Fish. Rev. 44: 2–3.
- Takemura, A., N. Nishida, and Kobayashi, Y. 1988. The attraction effect of natural feeding sound in fish. Bull. Fac. Fish. Nagasaki Univ. Chodai Suikenpo no. 63: 1–4.
- Tavolga, W. N. 1971. Sound production and detection. Pages 3–36 *in* W. N. Tavolga. Doeden, Hutchinson, and Ross, Inc., ed. Sound reception in fishes. Stroudsburg, Pennsylvania. 317 p.
- Turner, C. H., E. E. Ebert, and R. R. Given. 1969. Man-made reef ecology. Calif. Dept. Fish and Game. Fish Bull. 146: 1–221.
- Valentry, D. 1968. Sea-going trolleys. Sea Frontiers 14: 31.
- Wendt, P. H., D. M. Knott, and R. F. Van Dolah. 1989. Community structure of the sessile biota on five artificial reefs of different ages. Bull. Mar. Sci. 44: 1106–1122.
- Wenner, C. A., W. A. Roumillat, and C. W. Waltz. 1986. Contributions to the life history of black sea sass, *Centropristis striata*, off the southeastern United States. Fish. Bull. 84: 723–741.
- Wilkins, R. M. and M. H. Goodwin. 1989. Progress report on the evaluation of fish aggregation devices for the eastern Caribbean. Proc. 39th Ann. Gulf Carib. Fish. Inst., Hamilton, Bermuda, November 1986. Vol. 39: 405–407.
- Workman, I. K., A. M. Landry, Jr., J. W. Watson, Jr. and J. W. Blackwell. 1985. A midwater fish attraction device study conducted from hydrolab. Bull. Mar. Sci. 37: 377–386.
- Zahary, R. G. and M. J. Hartman. 1985. Artificial marine reefs off Catalina Island: recruitment, habitat specificity, and population dynamics. Bull. Mar. Sci. 37: 387–395.
- Zar, J. H. 1984. Biostatistical analysis. 2nd ed. Prentice Hall, Englewood Cliffs, New Jersey. 718 p.

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